Appendix 2. Preliminary Data collected on 2 February 2000. Trail length distances (as the ant walks, or as the bird flies to hole or focal point) do not correspond by row due to unclear records.

Colony ID	Forest Age	Nest Length	Nest Width	Nest Area	No.Active Holes	No.Other Holes	Distance Ant Travels from Tree to Hole (m)	Distance bird flies from Tree to Hole	Distance from Tree to Focal Point	dbh Harvest Tree	Morphospecies	Buttress?
A	S	15.27	4.6	70.2	4	13	11.5		17.4	31	5	Y
							8.4		6.4	61	6	Y
							6.2		10.1	40.1	7	Y
							12.6		9.6	46.3	8	N
							61.6		61.6	73.2	9	Y
							105.3		40.5	33.4	10	Y
							84		22.4	130.5	11	Y
							132.6			42.5	7	Y
B	S	11.4	7.2	82.1	5	60	33.8	28.6		13.6	1	N
							100.1	132.6		25.5	4	Y
							80.6	130.3		21.5	1	N
							39	39		15.8	1	N
							41.6	40.3		51.5	4	Y
							45.5	42.9		2	1	N
							51.4	13.9		33.6	12	N
B	P	16.06	4.38	70.3	1	12				57	15	Y
								22				
								4		85.9	16	Y
								52.6		127.3	14	Y
								69.7		49.3	13	Y
A	P	12.7	5.25	66.7	4	6	6.4		7.4	110	10	Y
							2.5		12.5	33	11	N
							16.5		7.9	11	12	N
							12.7		29	29.9211293	9	N
							7.6		15.6	45.20000384	11	N
							0.3		31.9	41.3802852	11	N
							29.2		44	63.66197724	10	Y
							11.4		57	28.64788976	11	N
							31.8		8.75	19.09859317	11	N
							45.7		4.3	35.33239737	11	N
							62.2		19.2	32.46760839	9	N
C	P	28.8	6.4	184	2	8	3.4			31.12	18	N
							37			25	17	N
							40			5	17	N
							58			0	17	N
							48			155	17	N

Resource partitioning in army ant bird communities

Maria S. Calvi, Megan K. Jennings, Michael D. Foote, and Laura R. Nagy

Abstract: Community theory predicts that resources should be partitioned to minimize interspecific competition. We tested for niche partitioning in the community of birds that forage in association with the continually moving swarms of foraging army ants. Ant bird species were non-randomly distributed in their horizontal perching positions relative to the ant swarm. Foraging height and foraging substrate were also significantly different among species. The number of successful foraging bouts averaged about 1.6 prey items • bird $^{-1}$ • 15 min $^{-1}$ for all species, indicating all species in the community accrue comparable benefits from their association with army ants. Other communities that also depend on mobile resources (e.g., bird communities of frugivorous altitudinal migrants that track seasonally fruiting trees) have solved similar challenges if they maintain niche partitions in spite of the dynamic spatial structure of their resource base.

*Key Words: barred woodcreeper (*Dendrocolaptes certhia*), bicolored antbird (*Gymnopithys leucaspis*) , chestnut-backed antbird, (*Myrmeciza exsul*),* Eciton burchelli, *gray-headed tanager (*Eucometis penicillata*), tawny-winged woodcreeper (*Dendrocincla anabatina*)*

Introduction

Species often compete for space and resources in natural communities. To minimize competition, coexisting species that utilize similar resources may partition these resources in space or time to reduce niche overlap. Normally, the resource base that is partitioned tends to be relatively fixed in space. However, birds that follow army ant swarms are an exception. These birds exploit the chaos induced by army ant foraging to feed upon fleeing arthropods. Because the location of the foraging ants constantly changes, the bird community must also move if they are to maintain an organized spatial structure.

Because multiple bird species forage over the same ant swarm and therefore are potentially competing for the same arthropod resources, community theory predicts that these resources should be partitioned. Coates-Estrada (1989) suggested that the bird species associated with army ants tend to partition space with respect to the position of the moving front of the foraging ant swarm. We hypothesized that the bird community associated with army ants has partitioned the resource base by foraging within different horizontal and vertical positions relative to the moving swarm of army ants. If ant bird assemblages are structured communities rather than random aggregations, it also follows that the bird species most closely associated with ant swarms would tend to have the highest foraging success and occupy the best foraging positions within the community.

Methods

We located a colony of the army ant *Eciton burchelli* that was foraging between the Ollas and Espaveles trails at the La Sirena biological station in Corcovado, Costa Rica. An assemblage of birds was with the army ants. We studied this aggregation of birds on 4, 6, and 7 February 2000 from 15:20 to 16:00, 10:00 to 11:20 and 12:30 to 17:20, and 08:30 to 11:20, respectively.

At 15 min intervals during our observations, we mapped the horizontal and verti-

cal perching positions of every bird relative to the ant swarm. Birds were assigned to a horizontal perching position category of front, center, or periphery (Fig. 1). We also estimated the height above ground of each bird at the time of our visual scan. The 15 min interval was chosen because it was long enough that the birds had moved at least several times (and had to have moved to have retained the same position relative to the ants). Thus, this interval was long enough that it seemed reasonable to treat the scans as independent observations.

We also monitored the front and center of the flock continuously for foraging events and agonistic interactions among birds. For each successful foraging event, we recorded the species of bird, the height from which the foraging maneuver was initiated, the height and substrate where the prey item was caught, and, if seen, the length of the prey item (relative to bill length). For each agonistic behavior, we recorded the bird species that were participating and where those interactions took place relative to the ant swarm.

This ant colony utilized two distinct foraging strategies. Primarily, ants foraged in a single swarm ranging in size from 50 to 240 m^2. However, on 6 – 7 February 2000 we also observed ants foraging in multiple, narrow columns rather than one unified front. Analyses of foraging behavior used observations taken during both types of ant activity, but analyses of bird spatial positions were restricted to the more common situation of a single, foraging ant swarm (n = 23 position maps collected on 4, 6, 7 February).

We used chi-square goodness-of-fit statistics to test for differences among species in foraging substrate, number of successful foraging attempts per individual, and aggressive interactions between species. We used a one-way analysis of variance to test for differences among species in perching and foraging height.

Results

On 6 February 2000, we located the bivouac of the ant swarm by following a narrow column (≈ 3 cm wide) of ants returning to the bivouac. The bivouac was within hollow spaces of a decomposing log. When the entire colony was present, it filled ≈ 31 dm^3. Ants were removing pupal cases on the morning of 7 February, indicating that this colony was nearing the end of a statatory reproductive phase, which is reported to last 17 – 22 d for this species. On 7 February, the day on which most of our data were collected, the first foraging column left the bivouac at 08:30. By 09:00, the ants had organized themselves into a foraging swarm that headed in a westerly direction from the bivouac. By 09:45, the area occupied by foraging ants (Fig. 1) was ≈ 10 x 15 m, which remained relatively constant (range = 7 x 15 m to 12 x 20 m) until we ceased observations at 11:15. The foraging swarm

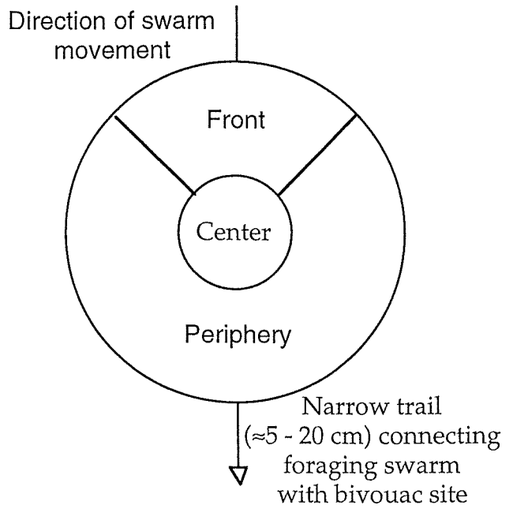

Figure 1. Possible bird locations relative to army ant swarms. Every 15 min during observation periods, we recorded which of these three positions was occupied by each bird. Birds foraging in association with the ant swarm were assigned map locations.

moved ≈ 57 m from the bivouac site over 2:45 h. The rate of movement ranged from 1 - 7 m / 15 min.

We observed five species of ant birds foraging in association with the ant swarm. Of these, the only species that is reported to be an obligate associate of army ants was the bicolored antbird (*Gymnopithys leucaspis*), which was also the most abundant species (up to 9 individuals). Other species were gray-headed tanagers (*Eucometis penicillata;* up to 3 individuals), tawny-winged woodcreepers (*Dendrocincla anabatina;* up to 2 individuals) and barred woodcreepers (*Dendrocolaptes certhia;* up to 1 individual; Fig. 2). On the morning of 7 February, the bicolored antbird was the first species to join the swarm. The tawny-winged woodcreeper, a banded individual which had been observed on previous days with the same ant swarm, arrived as the swarm began to move in a unified front and was followed shortly by the barred woodcreeper. Gray-headed tanagers tended to pass in and out of the swarm throughout the morning of 7 February, but were foraging continually with the swarm for at least 1.5 h during the previous afternoon. All four of these species were foraging on the invertebrates that were being flushed by the army ants. One individual of the chestnut-backed antbird (*Myrmeciza exsul*), another species reported to regularly forage with army ants, was associated with our ant swarm for ≈ 15 min during our observations. The chestnut-backed antbird, was not included in the analyses that follow.

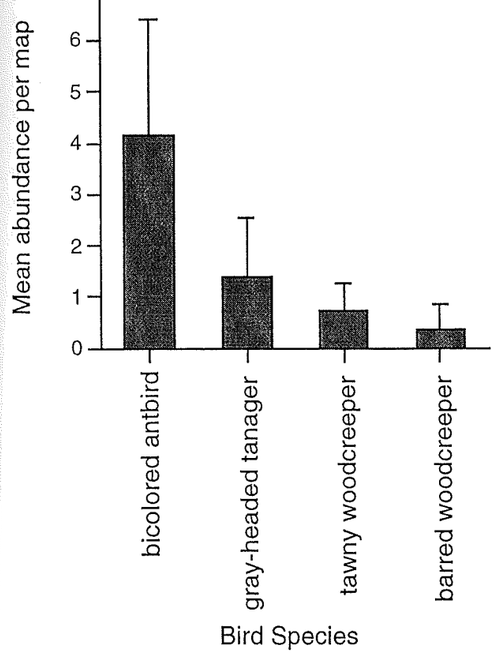

Figure 2. Mean abundance (± SD) of four bird species within a swarm of foraging ants at Corcovado National Park, Costa Rica. Data are based on 23 scans (15 min apart) conducted on 4, 6 - 7 Feb 2000.

Bird species were non-randomly distributed in their horizontal perching positions relative to the ant swarm (Table 1; G = 15.82, P = 0.02). Bicolored antbirds were over-represented in the periphery of the swarm while tawny-winged and barred woodcreepers were under-represented in the periphery. Tawny-winged woodcreepers tended to position themselves in the front and center of the swarm while the barred woodcreeper was usually in the center. Bicolored antbirds perched significantly lower to the ground than tawny-winged and barred woodcreepers (Fig. 3; $F_{3, 124} = 7.07$, P = 0.0002).

Foraging height and foraging substrate both differed among species ($F_{3, 168} = 189.84$, P < 0.0001; G = 27.8, df = 3, P < 0.0001, respectively). Eighty-four percent of all foraging attempts were initiated from foraging heights < 0.5 m high. The barred woodcreeper foraged from a significantly higher starting point than the other three species (Fig. 4). Eighty-seven percent of all prey captures occurred on the ground. However, tawny-winged and barred woodcreepers were often foraging on trunks (Table 2). The number of successful foraging bouts averaged about 1.6 prey items

Table 1. The number of bird observations at three horizontal positions in the ant swarm (based on the sum from 23 maps recorded at 15 min intervals). Parenthetical values indicate the expected frequencies if birds were randomly distributed with respect to species.

Bicolored antibrd	Gray-headed tanager	Tawny-winged woodcreeper	Barred woodcreeper	
Front	25 (27.4)	10 (9.0)	7 (4.9)	2 (2.7)
Center	29 (34.9)	11 (11.4)	9 (6.2)	7 (3.5)
Periphery	47 (38.7)	12 (12.6)	2 (6.9)	1 (3.8)

• bird $^{-1}$ • 15 min $^{-1}$ and was not significantly different among species ($X^2 = 9.34$, df = 6, p = 0.16). Aggressive interactions involving tawny-winged woodcreepers averaged about 0.6 interactions • bird $^{-1}$ • 15 min $^{-1}$, which was significantly higher than for the other species, especially bicolored antbirds which engaged in far fewer aggressive interactions than expected based on their abundance (Table 3; $X^2 = 24.62$, df = 1, p < 0.0001). All aggressive interactions of the barred woodcreepers were with tawny-winged woodcreepers, but data were not included in the chi-square test because there was only one barred woodcreeper and three interactions.

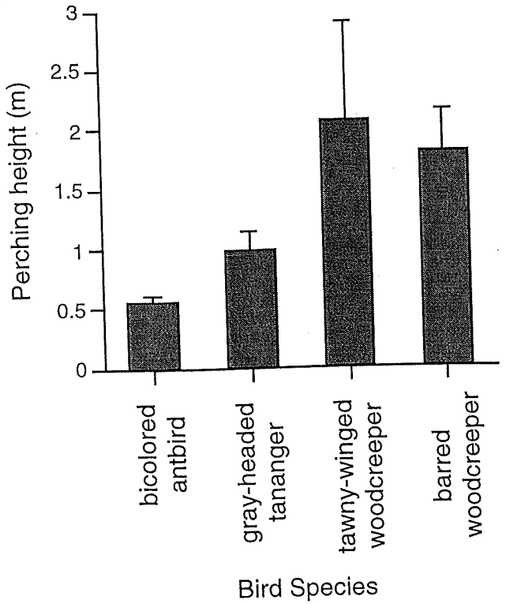

Figure 3. Perching height (± SE) of four bird species foraging within an army ant swarm (based on the average result from up to 23 scans, each of which was an average of all birds present at the time).

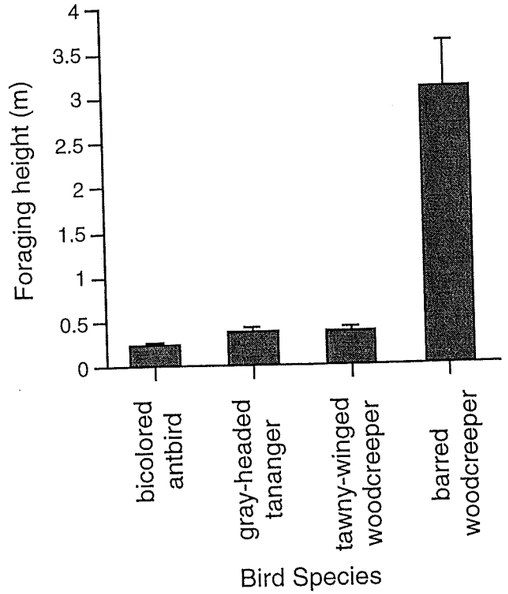

Figure 4. Average foraging height (± SE) of four bird species associated with an army ant swarm. Data describe the height of a bird directly before the maneuver that led to a successful prey capture (n = 12 - 79 observation / species).

Discussion

Species within an ant bird community appear to occupy different niches as defined

Table 2. The number of successful foraging bouts by substrate (ground, trunk or other) for four bird species associated with an army ant swarm.

	Bicolored antibrds	Gray-headed tanager	Tawny-winged woodcreeper	Barred woodcreeper
Ground	73	34	29	5
Other	1	2	0	0
Trunk	1	3	10	7
Sum	75	39	39	12
Bird observation units [a]	54	21	16	9
Expected [b]	89.1	34.65	26.4	14.85

[a] Average number of individual birds in front or center of swarm (see Fig. 1), which was the focal area for foraging events, multiplied by the number of 15 min observation periods (23).
[b] Based on the null hypothesis that bird species did not differ in their foraging success (i.e., foraging events • bird^{-1} • 15 min^{-1} was the same)

by their horizontal and vertical positions relative to the ant swarm. The central position of the swarm may be the most rewarding location because the high density of ants in the center seems to flush out many insects, which are then exposed to the foraging birds (Coates-Estrada 1989). This preferred position was most frequently occupied by the tawny-winged and the barred woodcreepers. These two relatively large species may be actively excluding other individuals from the center of the swarm; 74% of conflicts involved woodcreepers interacting with bicolored antbirds and gray-headed tanagers (Table 3). Species also partition space vertically through their use of different perching heights (Figure 3). For example, bicolored antbirds were primarily perched close to the ground while the woodcreepers perched higher in the canopy.

Despite the vertical structuring of foraging height, all birds except the barred woodcreeper tended to capture prey items close to the ground. Because prey were usually located on or in the leaf litter, foraging on the ground may maximize the view of fleeing insects and decrease the traveling distance to

Table 3. The number of observations of aggressive interactions among four bird species associated with an army ant swarm. Columns indicate one participant and rows indicate the other.

	Bicolored antbird	Gray-headed tanager	Tawny-winged woodcreeper	Barred woodcreeper
Bicolored antbird	2	0	6	0
Gray-headed tanager	0	2	4	0
Tawny-winged woodcreeper	1	0	0	3
Sum	3	2	10	3
Expected[a]	8.10	3.15	2.40	1.35

[a] Based on the null hypothesis that species did not differ in their propensity for aggressive interactions (i.e., interactions • bird^{-1} • 15min^{-1} was the same). Bird observation units same as in Table 2.

capture prey. This strategy may be more energy efficient and effective in competing with the ants and other birds for the same food resource. In contrast, barred woodcreepers apparently prefer to forage from higher substrates. They utilize their climbing ability to capture insect prey that have moved up tree trunks, where they would be inaccessible to bicolored antbirds and gray-headed tanagers. Although tawny-winged woodcreepers foraged on trunks as well, barred woodcreepers dominated the higher vertical positions, perhaps excluding the tawny-winged woodcreepers from these heights by virtue of their greater body size.

The similarity of prey capture rates for all species suggest that direct competition does not limit foraging success in this community. The majority of prey captures were approximately equal to the bill length of the bird, so bird species that differ in bill size apparently differ in prey size selection. These results suggest that the birds have partitioned the resources provided by army ants through differences in both spatial distribution and prey selection.

Although the position of resources change rapidly with the movement of the army ant swarm, ant bird community structure is maintained. Because all species are comparable competitors, we would predict that larger swarms would support a greater number of individuals in the same relative proportions.

Resource bases that move in space are not unique to army ant communities. Other bird communities, such as frugivorous altitudinal migrants, are also challenged to continually readjust their position in response to the changing spatial patterns of fruiting trees. Similarly, mobile resources are also common in other systems, such as piscivores feeding on mobile schooling fish and large terrestrial predators that follow migrating ungulate communities across savannas. If these communities are like the antbirds, then they retain their structure of niche partitioning even as they and their resources move. This partitioning presumably allows them to harvest their resource base more completely and efficiently than if the organization of the community were continually disrupted by the movement of resources.

Literature Cited

Coates-Estrada, R. and A. Estrada. 1989. Avian attendance and foraging of army ant swarms in the tropical rain forest of Los Tuxtlas, Veracruz, Mexico. Journal of Tropical Ecology 5: 281 – 292.